



# Landscape-scale drivers of fish faunal homogenization and differentiation in the eastern United States

Brandon K. Peoples · Amy J. S. Davis · Stephen R. Midway · Julian D. Olden · Lauren Stoczynski

Received: 31 August 2019 / Revised: 4 December 2019 / Accepted: 11 December 2019  
© Springer Nature Switzerland AG 2020

**Abstract** Establishment of nonnative fishes and extirpations of native fishes have homogenized freshwater fish faunas, yet our understanding of the drivers of this process remain limited. We addressed this knowledge gap by testing three hypotheses about introductions and homogenization of fish communities in the eastern United States: First, whether nonnative fish introductions have caused fish faunas to become homogenized or differentiated; second, whether patterns of faunal change are related to native species richness, propagule pressure, and anthropogenic disturbance; third, whether invasion patterns are attributable to either biotic resistance or preadaptation. We compared taxonomic similarity among watersheds

in historical and contemporary time steps, and modeled contributions of different drivers to faunal change within watersheds. Average similarity among watersheds nearly doubled in contemporary times, pointing to substantial fish faunal homogenization. No watersheds lost species; patterns of homogenization are attributable entirely to nonnative species invasion. Community change and nonnative richness were positively associated with agriculture-urban land use, recreational fishing demand, and elevation. Native richness negatively affected community change and nonnative richness. Nonnative species originated from watersheds with higher richness than the ones they invaded, suggesting a role for biotic resistance. Understanding how mechanisms operate across spatial scales will help guide future conservation efforts.

---

Guest editors: André A. Padiál, Julian D. Olden & Jean R. S. Vitule / The Aquatic Homogenocene.

---

B. K. Peoples (✉) · L. Stoczynski  
Dept. of Forestry & Environmental Conservation,  
Clemson University, Clemson, SC 29634, USA  
e-mail: peoples@clemson.edu

A. J. S. Davis  
Terrestrial Ecology Unit, Department of Biology, Ghent  
University, Ghent, Belgium

S. R. Midway  
Dept. of Oceanography and Coastal Sciences, Louisiana  
State University, Baton Rouge, LA 70803, USA

J. D. Olden  
School of Aquatic and Fishery Sciences, University of  
Washington, Seattle, WA 98105, USA

**Keywords** Stream · Species introductions · Biotic resistance · Propagule pressure · Freshwater · Nonnative species · Watersheds

## Introduction

Human activities have caused a global biodiversity crisis (Pimm et al., 1995; Vitousek et al., 1997). A key component of this crisis is biotic ‘homogenization’ (McKinney & Lockwood, 1999), in which species composition of regional communities become more

similar through time via loss of unique native species (or traits, alleles, etc.) and/or gain of shared nonnative species (Olden & Poff, 2003, 2004). Consequently, the homogenization process results in contemporary regional communities that are less distinct and which differ from their historical compositions. Biotic homogenization has become so prevalent that many authors consider modern times as the ‘Homogocene’ era of a ‘New Pangea’ (Rosenzweig, 2001). Homogenization is a particularly acute phenomenon for freshwater fishes (Scott & Helfman, 2001), especially via widespread introduction of nonnative species (Rahel, 2000).

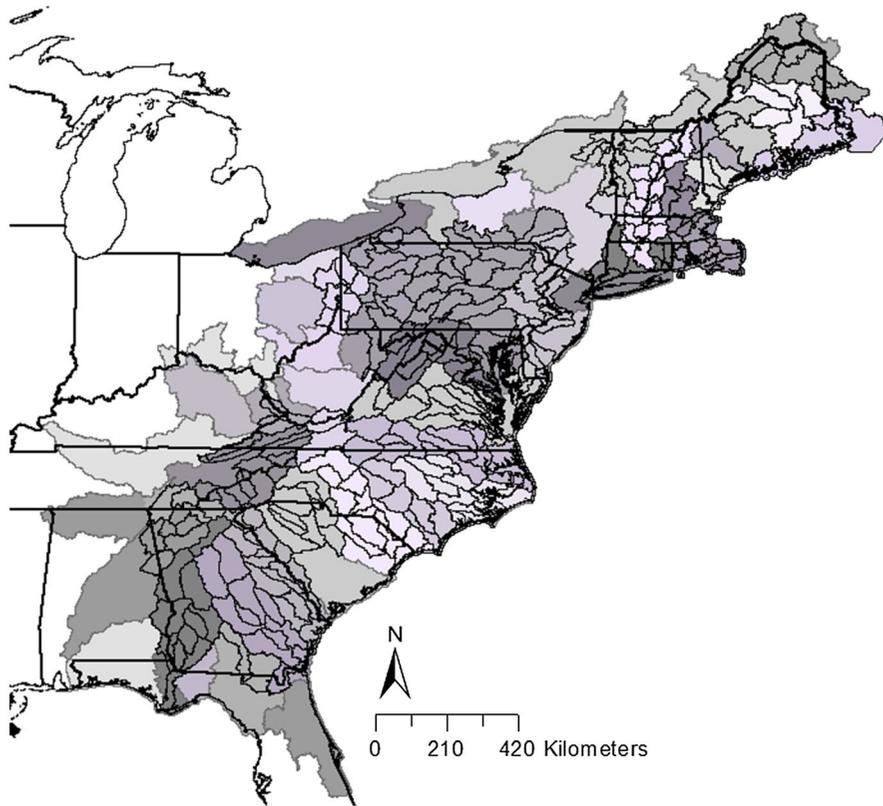
Perhaps because of high levels of diversity, endemism, and uniqueness of regional fish faunas, freshwater fishes are among the most prevalent taxa examined in the context of homogenization (Olden et al., 2018). Despite considerable advances in our quantification of fish faunal homogenization among various regions and spatial scales (Rahel, 2000; Taylor, 2004; Olden et al., 2008), a persistent research challenge is to identify and quantify the mechanisms underlying both the homogenization and differentiation process (Olden, 2006; Olden et al., 2018). Gaining such an understanding will help to better predict and prevent further biodiversity loss via homogenization.

Recent progress from the field of invasion ecology (a key component of homogenization) provides a simple framework that may inform mechanistic studies of homogenization. Invasions are stage-based processes (Blackburn et al., 2011) consisting of three basic components: propagule pressure/dispersal, abiotic factors, and biotic factors (the PAB framework; Catford et al., 2009). Propagule pressure is a suite of mechanisms indexing introduction effort (Lockwood et al., 2005), and is one of the most consistent predictors of invasions (Lockwood et al., 2009; Simberloff, 2009). Numerous studies have linked metrics indexing propagule pressure to a variety of metrics indexing invasions (Marchetti et al., 2004b; Marr et al., 2010). Because it focuses solely on human-mediated introduction effort, propagule pressure has been presented as a null model to test patterns of species invasions (Colautti et al., 2006). However, recent work suggests that it is contextualized by biotic and abiotic factors (Maurel et al., 2016; Peoples & Goforth, 2017a). Abiotic mechanisms such as disturbance or resource pulses facilitate invasions by creating novel niches disfavoring natives and allowing

colonization of nonnative species with unique traits (Hiero, et al. 2005). Furthermore, climatic similarity between a species’ native and nonnative ranges can explain invasion success as it is strongly linked with environmental compatibility with the nonnative range (Herborg et al., 2007).

Biotic factors refer to the role of organisms in the invasion process, and are among the most well-studied invasion mechanisms. Much research has elucidated the role of native species for inhibiting or facilitating introductions, often analyzed as relationships between native and nonnative species richness. The concept of ‘biotic resistance’ suggests that negative biotic interactions with native species in species-rich communities inhibits invasions, resulting in a negative relationship between native and nonnative species richness (Kennedy et al., 2002). In which case, successful nonnative species are transported from regions of higher richness than the recipient system, giving them a competitive advantage (Fitzgerald et al., 2016). On the other hand, nonnative richness may be positively associated with native richness because both nonnative and native species share similar traits, and thus demonstrate common ‘preadaptation’ to the recipient system (Thuiller et al., 2010). Because both concepts are well-supported by empirical evidence, this ‘invasion paradox’ can arise from contrasting mechanisms across spatial scales (Fridley et al., 2007).

In this study, we applied the PAB framework to quantify mechanisms driving temporal changes in stream fish communities via species introductions in streams of the eastern US (Fig. 1). We addressed three hypotheses concerned with fish species invasions and present-day changes in the eastern United States. First, we quantified differences in historical and contemporary fish assemblages at the watershed scale to test whether nonnative fish introductions have caused fish faunas to become homogenized or differentiated in space. Second, we used variables indexing PAB mechanisms to model fish assemblage change through time to test whether patterns of faunal change are related to spatial variation in native species richness, propagule pressure, and anthropogenic disturbance. Third, we explored relationships between richness in the native and nonnative ranges of nonnative species to test whether invasion patterns are attributable to either biotic resistance or preadaptation.



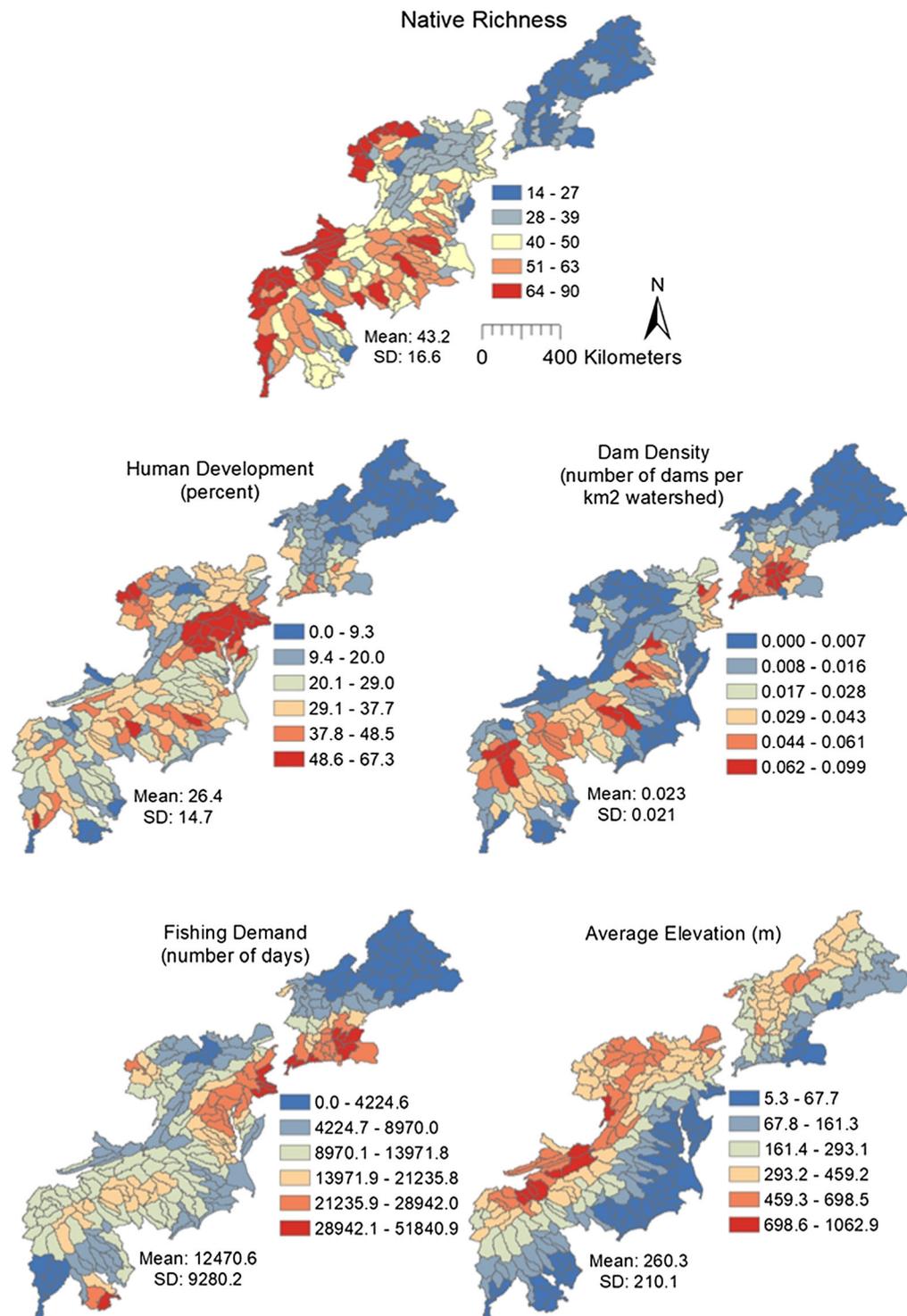
**Fig. 1** Our study area encompasses 12 states in the eastern US. 297 HUC8 watersheds (thin lines) are nested within 36 HUC4 watersheds (shaded). HUC4 colors are used only to illustrate their boundaries; they do not connote attributes

## Methods

### Study region and fish data

We conducted this study in 297 watersheds in 13 states of the eastern US (Fig. 1). This is an ideal region for addressing these questions because of high fish diversity (nearly 300 species), and numerous watersheds that are nearby in overland distance but largely disconnected by watercourse distance. Most watersheds in this region are in the Atlantic coast drainage, with headwaters originating the Appalachian Mountains and flowing eastward, although some watersheds occur in the Mississippi River and Great Lakes basins. Land cover is diverse in the region, with combinations of eastern deciduous forest, moderate to heavy row crop and pastoral agriculture, and suburban/urban development. Over 22,000 dams occur in the study area, ranging from small run-of-river barriers to large impoundments (Fig. 2).

Watersheds are hierarchical, and are classified using hydrologic unit codes (HUCs; Seaber et al., 1987). This study was conducted at the HUC8 scale (watersheds of 3500 to 4000 km<sup>2</sup>), the smallest scale at which native or nonnative status can reasonably be assigned to a species. We used the NatureServe Digital Distribution of Native Fishes by US watershed (NatureServe, 2010) to determine ‘historical’ watershed-scale occurrences. NatureServe collects and evaluates data from numerous sources, including the primary and secondary literature, agency sampling, and expert professional consultation. These data are reviewed by professional taxonomists and ecologists with in-depth expertise on regional fish biogeography. The stringent review process greatly decreases chances of major errors in assignment of native status. This dataset thus represents the best possible information on native stream fish distribution at the HUC8 scale before widespread introductions by European settlers, and has been used in numerous other biogeographic studies to represent native freshwater fish



**Fig. 2** Summarized abiotic variables at the HUC8 scale used for analyses

diversity (Muneepeerakul et al., 2008; Guo & Olden, 2014; Davis & Darling, 2017).

To identify species establishment at the HUC8 scale, we compared the NatureServe data to a dataset of contemporary (e.g. since the mid-1990s) stream fish community sampling conducted by state conservation or regulatory agencies. We included data from sampling programs based on strict criteria that: (1) they sampled stream reaches of sufficient length to characterize presence/absence (i.e. typically 20–30 times mean stream width or more; Moulton et al. 2002); (2) sampling and identification was done by professional biologists knowledgeable of the species and systems; and (3) the goal of the sampling was to characterize species richness and diversity (i.e. not targeting specific taxa, such as game species; see Peoples & Midway, 2018 for more information on specific data sources). The dataset consists of 139,184 unique locations on 13,267 stream segments (National Hydrography Dataset: COMIDs) in 297 watersheds within 12 US states. Because backpack electrofishing surveys can cause relatively low detection probabilities of some numerically rare species (Peoples & Frimpong, 2011; Pregler et al., 2015; Wagner et al., 2019), we only included watersheds in which  $\geq 15$  separate sites were sampled; this helped ensure that recently established but numerically rare nonnative species were detected.

A challenge associated with the historical data is that it may be influenced by instances of non-detection during historical sampling. For example, if a native species escaped detection, we would incorrectly conclude that species to be nonnative in that watershed. This issue could arise for a few species with naturally low abundance or highly restricted distributions within watersheds. However, we do not believe this potentially rare situation will affect analyses or conclusions because (a) NatureServe has made considerable effort to ensure data accuracy, (b) reach-scale contemporary data was coarsened to the HUC8 scale, reducing the likelihood of a misclassification, and (c) HUC8s are quite large and many have been sampled extensively throughout the historical dataset.

#### Abiotic variables

We calculated a suite of variables indexing PAB mechanisms (Fig. 2). Mean annual temperature was estimated using the near-global environmental

datasets for freshwater ecosystems calculated by Domisch et al. (2015), and mean elevation in each watershed was calculated according to the National Elevation Dataset (Gesch et al., 2002). We computed two variables to represent anthropogenic degradation. First, *percent developed land* was calculated as the cumulative proportion of land cover in a watershed being used as agriculture or urban/suburban using the 2011 National Land Cover Database (Homer et al., 2015). Second, *dam density* (number of dams per km<sup>2</sup> watershed)—an index of hydrological alteration (Pool & Olden, 2012)—was calculated from the National Inventory of Dams (USACE, 2018) (Fig. 2).

Using the approach described by Davis & Darling (2017), we used the modeled demand for freshwater fishing (*fishing demand*) as a metric of propagule pressure. *Fishing demand* in days was originally estimated at the 30-m pixel level and is based in part on the number of anglers likely to reside in that pixel based on the US Fish and Wildlife Service's National Survey of Fishing, Hunting, and Wildlife-Associated Recreation (FHWAR), combined with their willingness to travel, which was obtained from the US Forest Service National Visitor Use Monitoring (NVUM) program (Mazzotta et al., 2015). For this analysis, we summarized *fishing demand* by HUC8 (Fig. 2).

#### Analyses

To quantify fish faunal change over time *among watersheds*, we first calculated pairwise species similarity among all watersheds separately in each time step (hypothesis 1), then compared mean similarity between each time step. To quantify the drivers of faunal differentiation through time *within each watershed* (hypothesis 2), we calculated similarity between historical and contemporary species composition for each watershed. We indexed faunal similarity among watersheds using the Jaccard index ( $\beta_{JK}$ ):

$$\beta_{JK} = 1 - \frac{a_{JK}}{a_{JK} + b_E + c_K}$$

where  $a_{JK}$  is the number of species two watersheds has in common,  $b_J$  is the number of species unique to one watershed, and  $c_K$  is the number of species unique to the other watershed.  $\beta_{JK} = 1.0$  for watersheds with exactly similar composition, and 0 for watersheds with exactly dissimilar composition. In the equation above, the subscripts J and K represents different watersheds;

however, they can also represent different timesteps (within the same watershed).

Jaccard similarity represents beta diversity in the “broad sense” because it indexes change attributable to changes in richness and turnover—i.e., replacement of lost species without necessarily changing richness. Jaccard index has been criticized as a metric of taxonomic homogenization because it cannot differentiate between the influences of richness and turnover (Koleff et al., 2003; Leprieur et al., 2009; Baiser et al., 2012). However, we should note that in this dataset and at this spatial scale, we observed no species loss in any watershed. All species in the historical dataset were detected in the contemporary dataset. Moreover, in no case was species richness maintained through replacement (e.g. loss of one species replaced by another, Fig. 2). Thus, all changes in faunal composition were due to species additions. Because there is no turnover from species loss from historical to contemporary time steps, the most informative complement to assessing mechanism of faunal change ( $\beta_{JK}$ ) is to simply model nonnative richness for each watershed.

To model  $\beta_{JK}$  and nonnative richness, we first scaled and centred variables indexing PAB mechanisms (Fig. 2) to mean = 0 and standard deviation = 1. We screened for collinearity based on Pearson correlation ( $r$ ), variance inflation factor (VIF), and visual inspection of pairwise scatterplots. No unacceptable correlation was discovered (all  $r < 0.60$ ), but we removed *mean annual temperature* due to collinearity (VIF = 4.69). VIF was below 2.0 for the remaining variables. Using the *lme4* package in R version 3.4.3 (R Development Core Team, 2018), we fit a linear mixed model to estimate effects of PAB mechanisms on  $\beta_J$  between historical and contemporary communities, and included HUC4 as a random intercept. We then used the *glmmTMB* package (Magnusson et al., 2017) to fit a negative binomial generalized linear mixed model to estimate effects of PAB mechanisms on nonnative richness in each watershed, also including HUC4 as a random intercept. Nonnative richness was over-dispersed (mean = 9.5 species, variance = 25.9), but not zero-inflated; less than 5% of all records were zeroes.

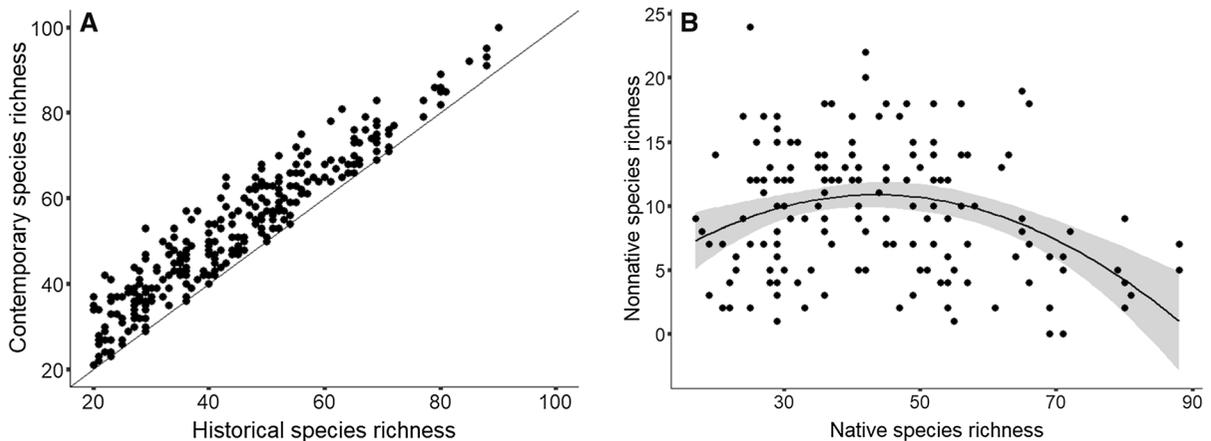
Finally, to further investigate the biotic resistance hypothesis, we sought to understand whether established nonnative species invade from watersheds with higher species richness than the nonnative watershed.

This hypothesis suggests species arriving from more diverse watersheds are generally more competitive and have an advantage over native species in less diverse watersheds (Sax & Brown, 2000; Fridley & Sax, 2014). To do so, we first identified all HUCs in which each species was native. Next, we calculated mean species richness in those watersheds so that each species was indexed by a value of native richness in its native distribution. We then calculated the mean richness in the native range of the suite of nonnative species in each watershed. For each invaded watershed, this represents the mean species richness of all watersheds from which each nonnative species arrived. We then calculated whether or not mean richness was higher in the native than the nonnative range, and the proportion of watersheds from which native richness was higher, then related these two metrics to native species richness.

## Results

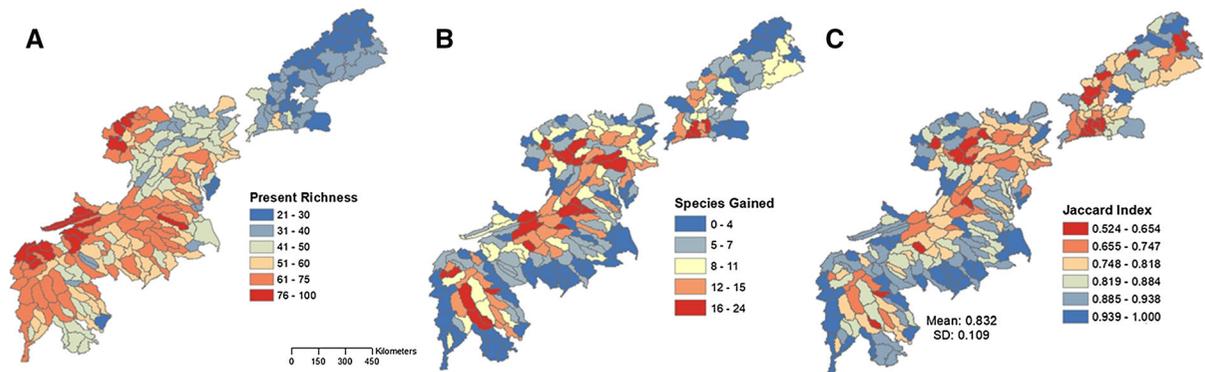
Introduction of nonnative species has significantly altered the biogeography of stream fishes in the eastern US by causing faunal homogenization among watersheds through time, as well as change in species composition within watersheds through time. All but eight watersheds demonstrated increases in species richness, and no watersheds lost species (Figs. 3, 4). Watersheds gained up to 24 species, with an average increase of  $8.2 \pm 0.30$  (SE) species. Watershed species richness grew as much as 91%, with an average increase of  $22\% \pm 0.10$ . Nonnative species now contribute up to half (47%) of total stream fish richness in some watersheds, with an average of  $17\% \pm 0.10$  (Fig. 4a, b). The relationship between native and nonnative richness was hump-shaped, with the largest difference occurring at moderate levels of native richness (30 species, Fig. 3b).

Watersheds became more homogenized through time. Pairwise faunal similarity among watersheds nearly doubled from  $0.37 \pm 0.002$  in the historical dataset to  $0.71 \pm 0.001$  in the contemporary dataset—an average increase of 34%. Of the 272 species in this study area, 184 (68%) were established outside of their native range elsewhere in the study area. The vast majority of nonnative species were translocated; only two exotic species were encountered in contemporary sampling: Brown Trout *Salmo trutta* and Common



**Fig. 3** **A** Number of species gained increased with historical species richness. The line represents a 1:1 relationship; points on the line represent watersheds that gained no species, and points above the line represent watersheds that gained species; no

watersheds lost species. **B** Relationship between nonnative and native species richness; the highest species gains occurred at moderate levels of species richness



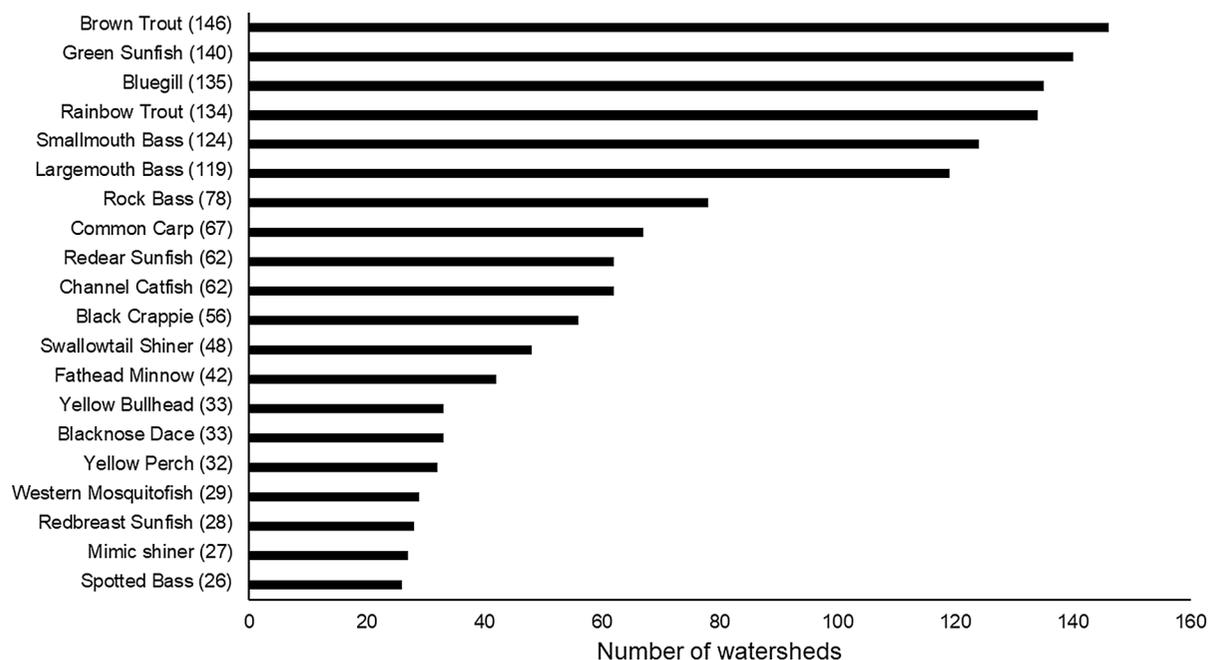
**Fig. 4** **A** Spatial patterns in contemporary species richness, **B** number of species gained, and **C** Jaccard similarity indexing change (comparison of historical and contemporary time

periods) in species composition due to species introductions. Low values of Jaccard index (reds) indicate higher faunal differentiation through time

Carp *Cyprinus carpio*. Translocated recreational fishes were the most prolific nonnative species; including Brown Trout (established in 146 watersheds), Green Sunfish *Lepomis cyanellus* (140 watersheds), Bluegill *L. macrochirus* (135 watersheds), Rainbow Trout *Oncorhynchus mykiss* (124 watersheds), Smallmouth Bass *Micropterus dolomieu* (125 watersheds), and Largemouth Bass *Micropterus salmoides* (119 watersheds). Most nongame nonnative fishes were encountered in fewer than 25 watersheds, but a few were widespread, including Swallowtail Shiner *Notropis procne* (48 watersheds) and Mimic Shiner *Notropis volucellus* (27 watersheds) (Fig. 5; Peoples & Midway, 2018).

On average, within-watershed similarity through time was  $0.83 \pm 0.01$ ; species introductions caused contemporary communities to change an average of 17%. Patterns of similarity and differentiation were variable across the landscape, with high differentiation in the Connecticut River basin (northeastern US), the Susquehanna River basin (central Pennsylvania), the upper Ohio River basin (North Carolina, Virginia), and the Altamaha River basin (Georgia). Coastal South Atlantic basins, as well as the Allegheny River basin (western Pennsylvania) gained fewer species and had higher similarity through time (Fig. 4c).

Within-watershed similarity through time was affected by a suite of PAB mechanisms.  $\beta_{JK}$  was affected negatively by *fishing demand*



**Fig. 5** The twenty most prolific nonnative species encountered in contemporary sampling, indexed by the number of watersheds in which they encountered outside their native range. Number of watersheds are in parentheses. Species include *Salmo trutta* (Linnaeus, 1758), *Lepomis cyanellus* (Rafinesque 1819), *Lepomis macrochirus* (Rafinesque, 1810), *Oncorhynchus mykiss* (Walbaum, 1792), *Micropterus dolomieu* (Lacépède, 1802), *Micropterus salmoides* (Lacépède, 1802), *Ambloplites rupestris* (Rafinesque, 1817), *Cyprinus carpio* (Linnaeus, 1758),

*Ictalurus punctulatus* (Rafinesque, 1818), *Lepomis microlophus* (Günther, 1859), *Pomoxis nigromaculatus* (Lesueur, 1829), *Notropis procne* (Cope, 1865), *Pimephales promelas* (Rafinesque, 1820), *Rhinichthys atratulus* (Hermann, 1804), *Ameiurus natalis* (Lesueur, 1820), *Perca flavescens* (Mitchell, 1814), *Gambusia affinis* (Baird and Girard, 1853), *Lepomis auritus* (Linnaeus, 1758), *Notropis volucellus* (Cope, 1865), and *Micropterus punctatus* (Rafinesque, 1819)

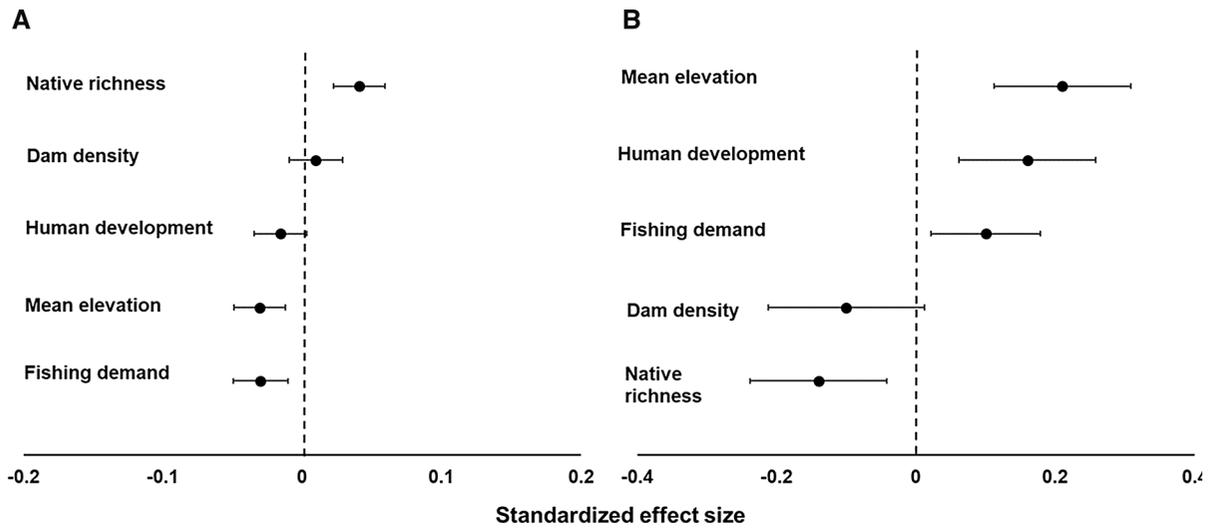
( $b = -0.03 \pm 0.009$ , SE) and *mean elevation* ( $b = -0.02 \pm 0.009$ ), and positively by *native species richness* ( $b = 0.05 \pm 0.008$ ). *Dam density* and *human development* had non-significant effects ( $b = 0.005 \pm 0.007$  and  $-0.02 \pm 0.010$ , respectively) (Fig. 3a). Effects of PAB mechanisms on nonnative richness were similar to those on  $\beta_{JK}$ . Nonnative richness was affected negatively by native richness ( $b = -0.14 \pm 0.05$ ), and positively by fishing demand ( $b = 0.10 \pm 0.04$ ), human development ( $b = 0.18 \pm 0.05$ ), and mean elevation ( $b = 0.21 \pm 0.05$ ). Only *dam density* had no significant effect on nonnative richness ( $b = 0.05 \pm 0.06$ ) (Fig. 6).

To further explore hypotheses of whether the significant effects of native richness represents a likely causal relationship (i.e. biotic resistance) or simply a statistical artefact (i.e. the regional species pool simply ‘running out of species’ in nonnative ranges), we related richness in the native range of all

species to native richness in each invaded watershed. On average, nonnative species came from more diverse watersheds than in their nonnative range for 79% of invaded watersheds, suggesting support for biotic resistance (Fig. 7a). However, there was a hump-shaped relationship between native richness and richness in native watersheds of nonnative species (Fig. 7b). Although much fewer in number, the invaded watersheds were on average most diverse between 50 and 60 native species.

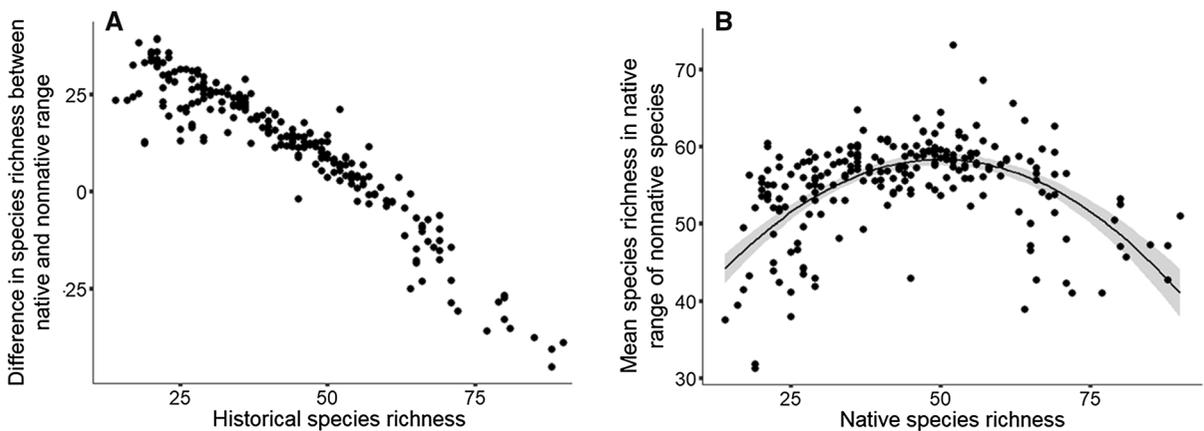
## Discussion

Streams and rivers of the eastern US are heavily invaded by nonnative fishes, reflected in substantial homogenization of fish faunas over time. Species richness has nearly doubled in some watersheds, and species composition has become nearly twice as similar among watersheds through time (from 37%



**Fig. 6** Standardized regression coefficients bounded by 95% confidence intervals of mechanisms indexing propagule pressure, abiotic factors, and biotic factors on **A** changes in faunal similarity through time ( $\beta_{JK}$ ) estimated with a linear mixed

model, and **B** nonnative species richness, estimated with a negative binomial mixed model. Effects with 95% CIs not bounding zero (dashed line) are interpreted as being statistically significant



**Fig. 7** **A** relationships between historical species richness and mean species richness in the native range of nonnative species. **B** Difference between mean richness in nonnative range (averaged among all species) and native richness in each watershed decreased with historical richness. Points above the

dashed line represent watersheds in which nonnative species come from richer watersheds (79% of watersheds); the remaining points below the line represent watersheds that are richer than those from which nonnative species originate

to 71%). Gains in species richness mirror those reported in other regions of the world. Among European river basins, Sommerwerk et al. (2017) found a mean net gain of  $5.7 \pm 4.1$  species per watershed, which is in the margin of error of our 8.2 species per watershed. Matsuzaki et al. (2013) observed higher richness increases than ours—2.4-

fold from historical times versus our maximum of 91%. Our observation of an average 34% increase in faunal similarity between historical and contemporary times is higher than broader-scale continental analyses. For example, Villéger et al. (2011) estimated global freshwater fish homogenization to be approximately 0.5%. Continental-scale analyses of

homogenization have estimated 2–5% among European basins (Villéger et al., 2014; Sommerwerk et al., 2017), 3% in Australia (Olden et al., 2008), 7% in China (Liu et al., 2017), 7.2% in the United States (Rahel, 2000), 1.3% in Canada, and up to 8.6% among Mediterranean regions across the world (Marr et al., 2010). Our observations of homogenization are higher, but more similar to regional analyses from California, USA (25%, Marchetti et al., 2001), 28% in British Columbia, Canada, (Taylor, 2004), and 17.1% in Iberia Peninsula (Clavero & Garcia-Berthou, 2006). Greater homogenization in our study area is likely facilitated by the close overland proximity but high fluvial separation of watersheds in our study area. This separation causes higher rates of endemism and faunal differentiation that can be easily disrupted by human dispersal networks, and having disproportionately large effects on of homogenization (McKinney, 2005).

Interestingly, only two species in this dataset are native to other continents (i.e. ‘exotic’; Brown Trout and Common Carp), and a handful are native to the western US Pacific slope (e.g. Rainbow Trout) or central US Mississippi River basin (e.g. catfishes *Ictalurus* spp., sunfishes *Lepomis* spp., and a few others). Accordingly, issues associated with potential contrasting patterns between exotic and translocated species are largely avoided (e.g. Marchetti et al., 2001; Smith, 2006). Almost all of these ‘long-distance’ invaders were transported deliberately by humans for sport fishing or other purposes (e.g. mosquito control), and these are among the most prolific in the region. However, the vast majority of nonnative species in our dataset are nongame fishes native to other watersheds in the study area that have been subsequently translocated, usually inadvertently, into adjacent watersheds (Peoples & Midway, 2018; Peoples et al., 2018). These ‘translocated’ nonnative species generally have stronger effects on homogenization because they are more commonly introduced due to geographic proximity (Matsuzaki et al., 2013; Sommerwerk et al., 2017; Villéger et al., 2014) and native range size (Marchetti et al., 2004b; Ribeiro et al., 2008). Considering this scale-based concept of native/non-native status will help better understand and prevent future homogenization of stream fish communities and the degradation of biodiversity (Leprieur et al., 2008b).

## Propagule pressure and abiotic factors

Fishing demand, our index of propagule pressure, had a significant relationship with patterns of fish faunal change over time. Watersheds with high fishing demand had greater numbers of established nonnative species and exhibit decreased similarity with other watersheds through time. Indices of propagule pressure are among the most ubiquitous predictors of invasion processes, related to patterns in establishment success (Marchetti et al., 2004c; Peoples & Goforth, 2017a), spread (Jeschke & Strayer, 2006), nonnative richness (Leprieur et al., 2008a; Davis & Darling, 2017), and homogenization (Clavero & Garcia-Berthou, 2006; Petsch, 2016). Moreover, human use is associated with invasiveness of most taxa, including freshwater fishes (Clavero & Garcia-Berthou, 2006; Dextrase & Mandrak, 2006; Kilian et al., 2012). Propagule pressure could swamp the effects of other mechanisms such as biotic resistance, preadaptation, habitat alteration, or climate matching (Lockwood et al., 2005). However, the effect of fishing demand on fish differentiation and nonnative richness were significant, albeit weaker than other variables examined in this study, leading us to suggest that propagule pressure is more likely contextual with other mechanisms (Pyšek et al., 2015; Maurel et al., 2016; Peoples & Goforth, 2017b).

In support of previous investigations, measures of human development were positively related to nonnative species richness. This is consistent with the general hypothesis that disturbance creates novel niches disfavoring native species and promoting colonization and establishment of nonnative species with novel traits (Olden et al., 2004; Strecker & Olden, 2014). Although we did not observe species loss at the HUC 8 watershed level, habitat-driven turnover at finer spatial scales (i.e. reach scale) likely facilitates establishment of nonnative species (Budnick et al., 2019). Surprisingly, we observed no significant association of dam density with changes in similarity or nonnative species richness. Dams generally facilitate invasions in streams by creating novel lentic habitats upstream, and disrupting the natural hydrologic regime downstream; both processes inhibit natives and promote nonnative species that lead to fish fauna homogenization (Johnson et al., 2008). Our finding suggests that dam density failed to adequately reflect hydrological alteration in our study area. Large

reservoirs are well known as hotspots for nonnative introductions (Clavero & Hermoso, 2011; Vitule et al., 2012) and many exist in our study area, but most of the dams in our study area create relatively small impoundments of a few hectares. Another explanation for our finding may be that most nonnative species in our study area are not novel lentic species, as have been observed in other studies (Pool & Olden, 2012). Instead, species prefer wadable streams and are no more tolerant of hydrological alteration in the nonnative range than in the native range.

Finally, mean elevation affected both faunal differentiation and nonnative species richness. This relationship likely reflects the interplay between species life history and the geophysical attributes of the study area, in which elevation generally increases from east to west. The elevational gradient creates a situation with more large rivers and reservoirs and fewer wadable streams in lower watersheds. Moreover, many of these streams are affected by saltwater intrusion from tidal areas. Stream fish diversity is naturally low in these habitats and largely represented by habitat generalists. The lower watershed habitat likely discourages colonization by species of the regional species pool better adapted for upland lotic systems. Stewart et al. (2016) found the opposite relationship between nonnative fish diversity and elevation in Wyoming, USA, largely because higher elevation streams are not suitable for many of the nonnative species in that system.

#### Native richness and biotic resistance

Native species richness had the strongest negative relationship with invasion patterns, lending evidence in favor of the biotic resistance hypothesis. First, native richness was positively associated with similarity between historical and contemporary time steps; richer communities were less likely to experience change due to species additions. However, this metric is not invariant of species richness, as the proportional role of single species additions is naturally lower in richer watersheds (Koleff et al., 2003). As a complement, we also found that the number of nonnative species was negatively affected by species richness. Because no watershed experienced turnover via species loss between time steps, nonnative richness represents a direct measure of faunal differentiation from species additions (Olden & Poff, 2003). Thus,

evidence supports that the positive effect of native richness is not an artefact of our choice of similarity index.

There is a possibility that association between native richness and faunal differentiation from species introductions is simply an artefact of the finite regional species pool, and not biotic resistance (Gido & Brown, 1999). Because the majority of nonnative species are native elsewhere in the study area, watersheds may simply ‘run out of species’ that have the potential to be nonnative. In this scenario, more depauperate watersheds receive nonnative species at a decreasing rate as richness approaches the regional species pool, whereas richer watersheds receive fewer nonnative species because many of those species are already native to that watershed. This scenario would suggest that biotic resistance is not a mechanism of resilience against invasion. However, if this were the case, we would expect no observed relationship between native richness in native and nonnative watersheds (Fridley & Sax, 2014; Fitzgerald et al., 2016). On the contrary, we found that nonnative species in most watersheds originate from generally more diverse watersheds than where they are introduced and established. Only the most diverse watersheds were invaded by species from more depauperate watersheds. Another aspect of this relationship is that the established and more prolific nonnative species in our study area had larger native range sizes (Peoples & Midway, 2018), which may be related to a suite of advantageous traits that facilitate colonization (Dawson et al., 2012; González-Suárez et al., 2015). Altogether, these findings suggest that in our study area and species pool, biotic resistance via interspecific competition may be a mechanism of watershed resilience against nonnative species invasions.

Relationships between native and nonnative richness are well studied, even among freshwater fishes. Interestingly, results have varied among taxonomic groups, study areas, and spatial scales. On the one hand, results from numerous studies suggest a role for biotic resistance in freshwater fish communities (Ricciardi & Atkinson, 2004; Vila-Gispert et al., 2005; Olden et al., 2006). On the other hand, positive relationships between native and nonnative diversity support a role for trait preadaptation (Gido et al., 2004; Marchetti et al., 2004a; dos Santos et al., 2018). Discrepancies among studies may be a function of spatial scale. For example, Guo & Olden (2014) found

contrasting relationships between native and nonnative richness in the same dataset at different scales. Inferring mechanism from pattern may be difficult, as different processes may be reflected at different scales. Moreover, the argument can be made that biotic interactions are inherently a fine-scale process, and can only be assessed with reach-scale observational studies (e.g. Stewart et al., 2016) or experiments (Alofs & Jackson, 2014); and not at watershed scales (Giam & Olden, 2016). Close attention should be paid to spatial scale when interpreting native-nonnative diversity relationships.

## Conclusions

Taxonomic and functional change through species loss and introductions represent a persistent challenge to maintaining biodiversity in the Anthropocene. The close overland distance and large fluvial separation of watersheds in the eastern US provides a unique system for examining faunal homogenization and differentiation. We observed no species loss from historical to contemporary times at the HUC8 scale, although turnover may be occurring at finer scales (i.e. HUC12s or reaches). The translocation of a few cosmopolitan sportfishes and many nongame species has caused communities to become overall nearly twice as similar to one another as they were historically. Native diversity may play a role in inhibiting differentiation from translocated species, but multi-scale approaches, including experiments, will be necessary for assigning causality to this mechanism.

**Acknowledgements** We thank the numerous agency and university employees who facilitated access to species occurrences. Comments by two anonymous reviewers greatly improved the manuscript. This article represents Technical Contribution Number 6814 of the Clemson University Experiment Station.

## References

- Alofs, K. M. & D. A. Jackson, 2014. Meta-analysis suggests biotic resistance in freshwater environments is driven by consumption rather than competition. *Ecology* 95(12): 3259–3270.
- Baiser, B., J. D. Olden, S. Record, J. L. Lockwood & M. L. McKinney, 2012. Pattern and process of biotic homogenization in the New Pangaea. *Proceedings of the Royal Society B: Biological Sciences* 279(1748): 4772–4777.
- Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. Wilson & D. M. Richardson, 2011. A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26(7): 333–339.
- Budnick, W. R., T. Lebourer, J. Belliard, J. Soininen, I. Lavoie, K. Pound, A. Jamoneau, J. Tison-Rosebery, E. Tales & V. Pajunen, 2019. Local and regional drivers of taxonomic homogenization in stream communities along a land use gradient. *Global Ecology and Biogeography* 2019: 1597–1609.
- Catford, J. A., R. Jansson & C. Nilsson, 2009. Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15(1): 22–40.
- Clavero, M. & E. Garcia-Berthou, 2006. Homogenization dynamics and introduction routes of invasive freshwater fish in the Iberian Peninsula. *Ecological Applications* 16(6): 2313–2324.
- Clavero, M. & V. Hermoso, 2011. Reservoirs promote the taxonomic homogenization of fish communities within river basins. *Biodiversity and Conservation* 20(1): 41–57.
- Colautti, R. I., I. A. Grigorovich & H. J. MacIsaac, 2006. Propagule pressure: a null model for biological invasions. *Biological Invasions* 8(5): 1023–1037.
- Davis, A. & J. Darling, 2017. Recreational freshwater fishing drives non-native aquatic species richness patterns at a continental scale. *Diversity and Distributions* 23(6): 692–702.
- Dawson, W., R. P. Rohr, M. van Kleunen & M. Fischer, 2012. Alien plant species with a wider global distribution are better able to capitalize on increased resource availability. *New Phytologist* 194(3): 859–867.
- Dextrase, A. J. & N. E. Mandrak, 2006. Impacts of alien invasive species on freshwater fauna at risk in Canada. *Biological Invasions* 8(1): 13–24.
- Domisch, S., G. Amatulli & W. Jetz, 2015. Near-global freshwater-specific environmental variables for biodiversity analyses in 1 km resolution. *Scientific Data* 2: 150073.
- dos Santos, D. A., D. J. Hoeinghaus & L. C. Gomes, 2018. Spatial scales and the invasion paradox: a test using fish assemblages in a Neotropical floodplain. *Hydrobiologia* 817(1): 121–131.
- Fitzgerald, D. B., M. Tobler & K. O. Winemiller, 2016. From richer to poorer: successful invasion by freshwater fishes depends on species richness of donor and recipient basins. *Global change biology* 22(7): 2440–2450.
- Fridley, J. D. & D. F. Sax, 2014. The imbalance of nature: revisiting a Darwinian framework for invasion biology. *Global Ecology and Biogeography* 23(11): 1157–1166.
- Fridley, J., J. Stachowicz, S. Naeem, D. Sax, E. Seabloom, M. Smith, T. Stohlgren, D. Tilman & B. V. Holle, 2007. The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88(1): 3–17.
- Gesch, D., M. Oimoen, S. Greenlee, C. Nelson, M. Steuck & D. Tyler, 2002. The national elevation dataset. *Photogrammetric Engineering and Remote Sensing* 68(1): 5–32.

- Giam, X. & J. D. Olden, 2016. Environment and predation govern fish community assembly in temperate streams. *Global Ecology and Biogeography* 25(10): 1194–1205.
- Gido, K. B. & J. H. Brown, 1999. Invasion of North American drainages by alien fish species. *Freshwater Biology* 42(2): 387–399.
- Gido, K. B., J. F. Schaefer & J. Pigg, 2004. Patterns of fish invasions in the Great Plains of North America. *Biological Conservation* 118(2): 121–131.
- González-Suárez, M., S. Bacher & J. M. Jeschke, 2015. Intraspecific trait variation is correlated with establishment success of alien mammals. *The American Naturalist* 185(6): 737–746.
- Guo, Q. & J. D. Olden, 2014. Spatial scaling of non-native fish richness across the United States. *PLoS ONE* 9(5): e97727.
- Herborg, L.-M., C. L. Jerde, D. M. Lodge, G. M. Ruiz & H. J. MacIsaac, 2007. Predicting invasion risk using measures of introduction effort and environmental niche models. *Ecological Applications* 17(3): 663–674.
- Hierro, J. L., J. L. Maron & R. M. Callaway, 2005. A biogeographical approach to plant invasions: the importance of studying exotics in their introduced and native range. *Journal of Ecology* 93(1): 5–15.
- Homer, C., J. Dewitz, L. Yang, S. Jin, P. Danielson, G. Xian, J. Coulston, N. Herold, J. Wickham & K. Megown, 2015. Completion of the 2011 National Land Cover Database for the conterminous United States—representing a decade of land cover change information. *Photogrammetric Engineering & Remote Sensing* 81(5): 345–354.
- Jeschke, J. M. & D. L. Strayer, 2006. Determinants of vertebrate invasion success in Europe and North America. *Global Change Biology* 12: 1608–1698.
- Johnson, P. T., J. D. Olden & M. J. Vander Zanden, 2008. Dam invaders: impoundments facilitate biological invasions into freshwaters. *Frontiers in Ecology and the Environment* 6(7): 357–363.
- Kennedy, T. A., S. Naeem, K. M. Howe, J. M. Knops, D. Tilman & P. Reich, 2002. Biodiversity as a barrier to ecological invasion. *Nature* 417(6889): 636–638.
- Kilian, J. V., R. J. Klauda, S. Widman, M. Kashiwagi, R. Bourquin, S. Weglein & J. Schuster, 2012. An assessment of a bait industry and angler behavior as a vector of invasive species. *Biological Invasions* 14(7): 1469–1481.
- Koleff, P., K. J. Gaston & J. J. Lennon, 2003. Measuring beta diversity for presence–absence data. *Journal of Animal Ecology* 72(3): 367–382.
- Leprieur, F., O. Beauchard, S. Blanchet, T. Oberdorff & S. Brosse, 2008a. Fish invasions in the world's river systems: when natural processes are blurred by human activities. *PLoS biology* 6(2): e28.
- Leprieur, F., O. Beauchard, B. Hugueny, G. Grenouillet & S. Brosse, 2008b. Null model of biotic homogenization: a test with the European freshwater fish fauna. *Diversity and Distributions* 14(2): 291–300.
- Leprieur, F., J. D. Olden, S. Lek & S. Brosse, 2009. Contrasting patterns and mechanisms of spatial turnover for native and exotic freshwater fish in Europe. *Journal of Biogeography* 36(10): 1899–1912.
- Liu, C., D. He, Y. Chen & J. D. Olden, 2017. Species invasions threaten the antiquity of China's freshwater fish fauna. *Diversity and Distributions* 23(5): 556–566.
- Lockwood, J. L., P. Cassey & T. Blackburn, 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution* 20: 223–228.
- Lockwood, J. L., P. Cassey & T. M. Blackburn, 2009. The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. *Diversity and Distributions* 15(5): 904–910.
- Magnusson, A., H. Skaug, A. Nielsen, C. Berg, K. Kristensen, M. Maechler, K. van Bentham, B. Bolker & M. Brooks, 2017. *glmmTMB: generalized linear mixed models using template model builder*. R package version 01 3.
- Marchetti, M. P., T. Light, J. Feliciano, T. Armstrong, Z. Hogan, J. Viers & P. B. Moyle, 2001. Homogenization of California's Fish Fauna Through Abiotic Change Biotic homogenization. Springer, New York: 259–278.
- Marchetti, M. P., T. Light, P. B. Moyle & J. H. Viers, 2004a. Fish invasions in California watersheds: testing hypotheses using landscape patterns. *Ecological Applications* 14(5): 1507–1525.
- Marchetti, M. P., P. B. Moyle & R. Levine, 2004b. Alien fishes in California watersheds: characteristics of successful and failed invaders. *Ecological Applications* 14(2): 587–596.
- Marchetti, M. P., P. B. Moyle & R. Levine, 2004c. Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology* 49(5): 646–661.
- Marr, S. M., M. P. Marchetti, J. D. Olden, E. Garcia-Berthou, D. L. Morgan, I. Arismendi, J. A. Day, C. L. Griffiths & P. H. Skelton, 2010. Freshwater fish introductions in mediterranean-climate regions: are there commonalities in the conservation problem? *Diversity and Distributions* 16: 606–619.
- Matsuzaki, S. I. S., T. Sasaki & M. Akasaka, 2013. Consequences of the introduction of exotic and translocated species and future extirpations on the functional diversity of freshwater fish assemblages. *Global Ecology and Biogeography* 22(9): 1071–1082.
- Maurel, N., J. Hanspach, I. Kühn, P. Pyšek & M. van Kleunen, 2016. Introduction bias affects relationships between the characteristics of ornamental alien plants and their naturalization success. *Global Ecology and Biogeography* 25(12): 1500–1509.
- Mazzotta, M., L. Wainger, S. Siffleet, J. T. Petty & B. Rashleigh, 2015. Benefit transfer with limited data: an application to recreational fishing losses from surface mining. *Ecological Economics* 119: 384–398.
- McKinney, M. L., 2005. Species introduced from nearby sources have a more homogenizing effect than species from distant sources: evidence from plants and fishes in the USA. *Diversity and Distributions* 11(5): 367–374.
- McKinney, M. L. & J. L. Lockwood, 1999. Biotic homogenization: a few winners replacing many losers in the next mass extinction. *Trends in Ecology & Evolution* 14(11): 450–453.
- Muneepeerakul, R., E. Bertuzzo, H. J. Lynch, W. F. Fagan, A. Rinaldo & I. Rodriguez-Iturbe, 2008. Neutral metacommunity models predict fish diversity patterns in Mississippi-Missouri basin. *Nature* 453: 223.
- NatureServe, 2010. *Digital Distribution Maps of the Freshwater Fishes in the Conterminous United States*, version 3.0. Arlington.

- Olden, J. D., 2006. Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography* 33(12): 2027–2039.
- Olden, J. D. & N. L. Poff, 2003. Toward a mechanistic understanding and prediction of biotic homogenization. *The American Naturalist* 162(4): 442–460.
- Olden, J. D. & N. L. Poff, 2004. Ecological processes driving biotic homogenization: testing a mechanistic model using fish faunas. *Ecology* 85(7): 1867–1875.
- Olden, J. D., N. L. Poff, M. R. Douglas, M. E. Douglas & K. D. Fausch, 2004. Ecological and evolutionary consequences of biotic homogenization. *Trends in Ecology & Evolution* 19(1): 18–24.
- Olden, J. D., N. L. Poff & K. R. Bestgen, 2006. Life-history strategies predict fish invasions and extirpations in the Colorado River Basin. *Ecological Monographs* 76(1): 25–40.
- Olden, J. D., M. J. Kennard & B. J. Pusey, 2008. Species invasions and the changing biogeography of Australian freshwater fishes. *Global Ecology and Biogeography* 17(1): 25–37.
- Olden, J. D., L. Comte & X. Giam, 2018. The Homogocene: a research prospectus for the study of biotic homogenisation. *NeoBiota* 37: 23.
- Peoples, B. K. & E. A. Frimpong, 2011. Among-pass, interregional, and single- versus multiple-season comparisons of detection probabilities of stream fishes. *Transactions of the American Fisheries Society* 140: 67–83.
- Peoples, B. K. & R. Goforth, 2017a. Commonality in traits and hierarchical structure of vertebrate establishment success. *Diversity and Distributions* 23(8): 854–862.
- Peoples, B. K. & R. R. Goforth, 2017b. The indirect role of species-level factors in biological invasions. *Global Ecology and Biogeography* 26(5): 524–532.
- Peoples, B. K. & S. R. Midway, 2018. Fishing pressure and species traits affect stream fish invasions both directly and indirectly. *Diversity and Distributions* 24(8): 1158–1168.
- Peoples, B. K., S. R. Midway, J. T. DeWeber & T. Wagner, 2018. Catchment-scale determinants of nonindigenous minnow richness in the eastern United States. *Ecology of Freshwater Fish* 27(1): 138–145.
- Petsch, D. K., 2016. Causes and consequences of biotic homogenization in freshwater ecosystems. *International Review of Hydrobiology* 101(3–4): 113–122.
- Pimm, S. L., G. J. Russell, J. L. Gittleman & T. M. Brooks, 1995. The future of biodiversity. *Science* 269(5222): 347–350.
- Pool, T. K. & J. D. Olden, 2012. Taxonomic and functional homogenization of an endemic desert fish fauna. *Diversity and Distributions* 18(4): 366–376.
- Pregler, K. C., J. C. Vokoun, T. Jensen & N. Hagstrom, 2015. Using multimethod occupancy estimation models to quantify gear differences in detection probabilities: is backpack electrofishing missing occurrences for a species of concern? *Transactions of the American Fisheries Society* 144(1): 89–95.
- Pyšek, P., A. M. Manceur, C. Alba, K. F. McGregor, J. Pergl, K. Štajerová, M. Chytrý, J. Danihelka, J. Kartesz & J. Klimešová, 2015. Naturalization of central European plants in North America: species traits, habitats, propagule pressure, residence time. *Ecology* 96(3): 762–774.
- Rahel, F. J., 2000. Homogenization of fish faunas across the United States. *Science* 288(5467): 854–856.
- Ribeiro, F., B. Elvira, M. J. Collares-Pereira & P. B. Moyle, 2008. Life-history traits of non-native fishes in Iberian watersheds across several invasion stages: a first approach. *Biological Invasions* 10(1): 89–102.
- Ricciardi, A. & S. K. Atkinson, 2004. Distinctiveness magnifies the impact of biological invaders in aquatic ecosystems. *Ecology Letters* 7(9): 781–784.
- Rosenzweig, M. L., 2001. The four questions: what does the introduction of exotic species do to diversity? *Evolutionary Ecology Research* 3(3): 361–367.
- Sax, D. F. & J. H. Brown, 2000. The paradox of invasion. *Global Ecology and Biogeography* 9(5): 363–371.
- Scott, M. C. & G. S. Helfman, 2001. Native invasions, homogenization, and the mismeasure of integrity of fish assemblages. *Fisheries* 26(11): 6–15.
- Seaber, P. R., F. P. Kapinos & G. L. Knapp, 1987. *Hydrologic Unit Maps*. US Government Printing Office, Washington, DC.
- Simberloff, D., 2009. The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution and Systematics* 40: 81–102.
- Smith, K. G., 2006. Patterns of nonindigenous herpetofaunal richness and biotic homogenization among Florida counties. *Biological Conservation* 127(3): 327–335.
- Sommerwerk, N., C. Wolter, J. Freyhof & K. Tockner, 2017. Components and drivers of change in European freshwater fish faunas. *Journal of Biogeography* 44: 1781–1790.
- Stewart, D. R., A. W. Walters & F. J. Rahel, 2016. Landscape-scale determinants of native and non-native Great Plains fish distributions. *Diversity and Distributions* 22(2): 225–238.
- Strecker, A. L. & J. D. Olden, 2014. Fish species introductions provide novel insights into the patterns and drivers of phylogenetic structure in freshwaters. *Proceedings of the Royal Society of London B: Biological Sciences* 281(1778): 20133003.
- Taylor, E. B., 2004. An analysis of homogenization and differentiation of Canadian freshwater fish faunas with an emphasis on British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences* 61(1): 68–79.
- Team, R. D. C., 2018. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna.
- Thuiller, W., L. Gallien, I. Boulangeat, F. De Bello, T. Münkemüller, C. Roquet & S. Lavergne, 2010. Resolving Darwin's naturalization conundrum: a quest for evidence. *Diversity and Distributions* 16(3): 461–475.
- United States Army Corps of Engineers, 2018. *National Inventory of Dams*.
- Vila-Gispert, A., C. Alcaraz & E. García-Berthou, 2005. Life-History Traits of Invasive Fish in Small Mediterranean Streams Issues in Bioinvasion Science. Springer, New York: 107–116.
- Villéger, S., S. Blanchet, O. Beauchard, T. Oberdorff & S. Brosse, 2011. Homogenization patterns of the world's freshwater fish faunas. *Proceedings of the National Academy of Sciences USA* 108(44): 18003–18008.
- Villéger, S., G. Grenouillet & S. Brosse, 2014. Functional homogenization exceeds taxonomic homogenization

- among European fish assemblages. *Global Ecology and Biogeography* 23(12): 1450–1460.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco & J. M. Melillo, 1997. Human domination of Earth's ecosystems. *Science* 277(5325): 494–499.
- Vitule, J. R. S., F. Skóra & V. Abilhoa, 2012. Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics. *Diversity and Distributions* 18(2): 111–120.
- Wagner, M. D., D. A. Schumann & B. J. Smith, 2019. Gear effectiveness and size selectivity for five cryptic madtom species (*Noturus* spp.). *Journal of Applied Ichthyology* 35(3): 673–682.

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.